



Tree-ring Reconstruction of Historic Insect Outbreaks in Lake Clark and Katmai National Parks and Preserves

Final Report

Natural Resource Technical Report NPS/SWAN/NRTR—2011/482



ON THE COVER

Spruce beetle-induced mortality in white spruce, Bay of Isles, Katmai National Park and Preserve.
Photograph by: Amy Miller, Southwest Alaska Network

Tree-ring Reconstruction of Historic Insect Outbreaks in Lake Clark and Katmai National Parks and Preserves

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Abstract

Recent spruce bark beetle (*Dendroctonus rufipennis*) activity in south-central and southwest Alaska has resulted in widespread mortality of mature white spruce. We used tree-ring data to examine the occurrence of and climatic influences on historic spruce beetle outbreaks at 15 sites on the Alaska Peninsula and compared our findings with known beetle activity on the Kenai Peninsula over the last 300 years. At each site, we collected stand structure data (i.e., species composition, density, and size structure) and tree cores for the determination of age structure, growth trends, and tree death dates. In addition, we compared our regional dataset of spruce beetle outbreaks across the Alaska Peninsula with three climate reconstructions that tracked (1) regional temperature and precipitation; (2) El Niño-Southern Oscillation (ENSO); and (3) the Pacific Decadal Oscillation (PDO) conditions. Our results indicate significant growth releases attributed to spruce beetle outbreaks in the 1810s, 1830s, 1870s, 1900-1910s, and late 1970s-early 1980s. These periods coincided with a previously published record of beetle activity on the Kenai Peninsula. Our study suggests that moderate to high severity spruce beetle outbreaks occurred episodically (mean return interval of 55 years) over the past 250 years across areas of south-central and southwest Alaska, and were associated with multi-year periods of warm and dry conditions related to El Niño and warm-phase PDO conditions. This apparent relationship between beetle activity and climate indicates that high-frequency (multi-year) climate variability has been the primary driver of widespread, epidemic-proportion outbreaks. The spatial extent of recent bark beetle activity appears to be within its historical geographic range, but outbreaks since the late 20th century show greater synchrony across sites than in the past, suggesting that the severity of the recent outbreak may be unprecedented.

Acknowledgments

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Introduction

Linkages between record breaking temperatures and drought conditions in the last decade are widely recognized as important drivers of recent increases in wildfire and insect outbreaks in forested ecosystems across western North America (e.g., Westerling et al. 2006, Raffa et al. 2008). Between 2000 and 2003, bark beetle-caused mortality in forests of the western U.S. increased from 1.6 million ha to 4 million ha, representing the largest annual increase in recorded history (Western Forestry Leadership Council - WFLC 2007). In addition, recent epidemic levels of beetle outbreaks have shown greater temporal synchrony and spatial expansion into new areas than previously observed during the 20th century (Raffa et al. 2008). The long-term effects of the extensive beetle damage are uncertain and could determine vegetation patterns in forested landscapes for centuries.

Widespread eruptions of bark beetle populations have occurred episodically in the past in western North America. Evidence of bark beetle outbreaks prior to the 20th century comes from a diversity of sites, including spruce (*Picea engelmannii*) forests in Colorado (e.g., Baker and Veblen 1990; Eisenhart and Veblen 2000, Kulakowski et al. 2003, Bebi et al. 2003; Bigler et al. 2005; Kulakowski et al. 2007) and Utah (Hebertson and Jenkins 2008), lodgepole pine (*Pinus contorta*) forests in southern British Columbia (e.g., Alfaro et al. 2004, Safranyik and Carroll 2006; Taylor et al. 2006), and white (*Picea glauca*) and Lutz (*Picea × lutzii*; a hybrid between *Picea glauca* × *Picea sitchensis*) spruce forests on the Kenai Peninsula of Alaska (Berg et al. 2006).

Recent studies have identified a link between 20th century insect infestations and inter-annual variation in weather (e.g., Berg et al. 2006; Hebertson et al. 2008), but our understanding of the relationship, if any, between broad-scale climate mechanisms operating at various time scales (e.g., decadal to multi-decadal vs. interannual variability) and beetle activity prior to the 20th century is limited. Recent studies indicate that sea surface temperatures and atmospheric pressure in both the north Pacific and north Atlantic Oceans influence regional climate in western North America (e.g. Gray et al. 2004; McCabe et al. 2004), and also affect regional variability in wildfire regimes (e.g., Westerling and Swetnam 2003; Grissino-Mayer et al. 2004; Hessl et al. 2004; Gedalof et al. 2005; Taylor and Beaty 2005; Schoennagel et al. 2004; Brown 2006; Kitzberger et al. 2006, Schoennagel et al. 2007; Sherriff and Veblen 2008). Similar, yet distinctly regional, climate influences would presumably also synchronize epidemic levels of spruce beetle activity, although no studies to date have explored long-term (i.e., pre-20th century) relationships between outbreaks and climate variability at a regional scale.

In North American high latitude forests, the spruce bark beetle (*Dendroctonus rufipennis*) is the most important agent of mortality (Ford 1986). South-central and southwest Alaska has experienced a regional outbreak of spruce bark beetle that has killed more than 1.2 million ha of spruce forest since 1989, with much of the mortality occurring on the Kenai Peninsula (Berg et al. 2006). In spite of recent spruce bark beetle activity on the Alaska Peninsula, we know little about the historic occurrence or causes of insect disturbance beyond that of the Kenai Peninsula. Of particular importance is information on the history of bark beetle activity in forests of Lake Clark and Katmai National Park and Preserves (hereafter referred to as Lake Clark and Katmai), as these stands span the transition from boreal to maritime ecosystems (Lake Clark), and

represent the southernmost extent of spruce forest on the Alaska Peninsula (Katmai). A recent tree-ring reconstruction of summer temperatures (1769-2003) derived from the northern Alaska Peninsula indicates a general warming in the region starting in the 1940s, with accelerated warming since the 1970s (Driscoll et al. 2005). The recent warming is believed to have contributed to the approximately 41,400 ha of forest damaged by the spruce beetle between 1989-2007 (Wittwer 2004; Lundquist 2007), as well as the spike in beetle activity in Katmai in 2006, where approximately 28,330 ha of mature spruce were affected (Lundquist 2007).

In this study, we examine the spatiotemporal occurrence of and climatic influences on historic (100-300 year chronologies) spruce bark beetle activity on the Alaska Peninsula and compare our findings with known beetle activity on the Kenai Peninsula. We address the following questions of relevance to long-term forest monitoring: (1) is there evidence of previous spruce bark beetle outbreaks on the Alaska Peninsula; (2) were historic insect outbreaks localized or synchronized across the landscape; and (3) are there detectable relationships between regionally synchronous insect outbreaks and climate variability at inter-annual to multi-decadal scales?

Methods

Field collections

We collected stand structure data (i.e., species composition, density and size structure) and tree cores (i.e., for age structure, growth trends and death dates) from 15 sites across the Alaska Peninsula (Fig. 1). We sampled seven sites in Lake Clark National Park and Preserve and two sites on Pedro Bay Native Corporation and Native Council land (Pedro Bay and Pile Bay) adjacent to Lake Iliamna in July 2005, and five sites in Katmai National Park and Preserve in July 2007 (Fig. 1). We also include the results from an additional site, previously sampled in 2000 (Berg et al. 2006), from the southern coast of Lake Clark (Polly Creek - PO; Fig. 1; Table 1). At each of the 15 sites, we used standard methods (Fritts 1976, Cook et al. 1990, Berg et al. 2006) to collect 65-121 cores from both live and dead trees (Table 1). The sites span a north-south gradient of approximately 300 km, and an east-west gradient of 160 km.

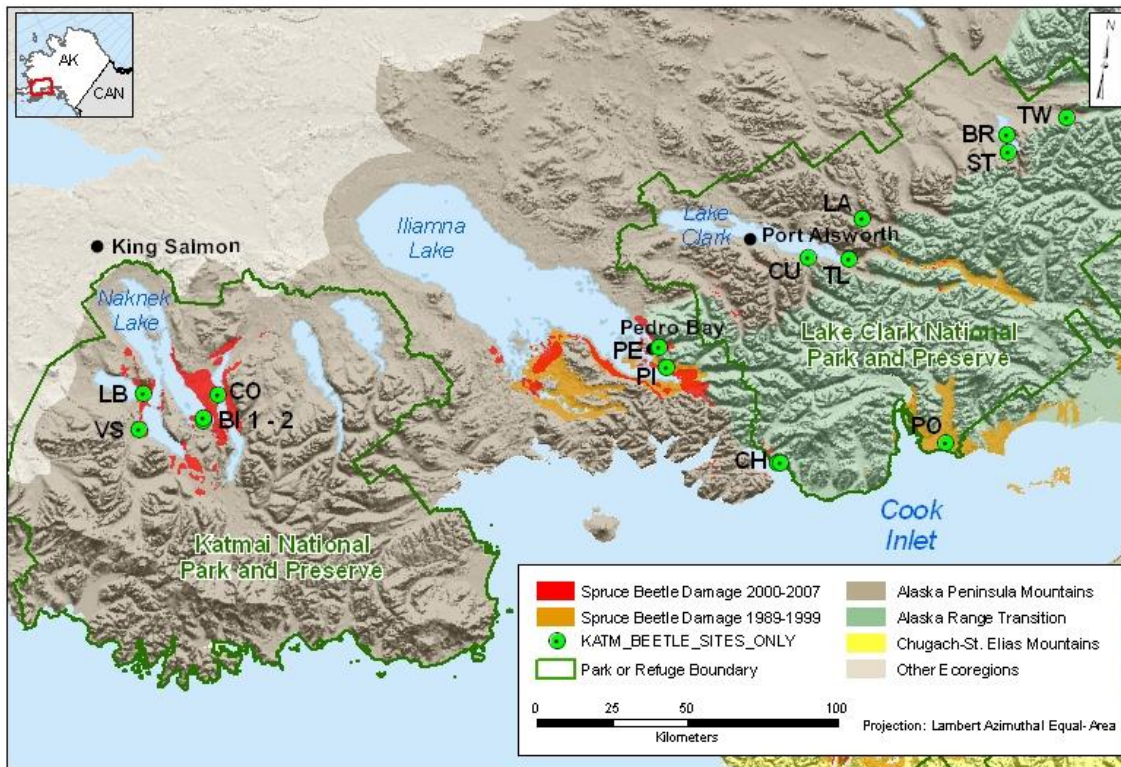


Figure 1. Study sites in Lake Clark and Katmai National Park and Preserve.

Our sites were chosen to meet specific criteria (primarily high stand density, composition and age) under which we could reconstruct past beetle history using dendroecological methods (e.g., Veblen et al. 1991, Berg et al. 2006). The sites ranged in size from approximately 10 to 50 ha, depending on local conditions, and were representative of the range of forested areas that had been affected by the current spruce beetle outbreak (low to high-severity infested stands). We sampled in relatively homogeneous, mature, closed-canopy stands of white spruce, with the exception of Chinitna Bay and Polly Creek, where we sampled in closed stands of Lutz spruce (*Picea × lutzii*; a hybrid between *Picea glauca* × *Picea sitchensis*). At each site, a minimum of

65 tree cores (median of 91; Table 1) were collected at a minimum distance of 10 m (33 feet) from one another, below treeline, and away from areas of obvious disturbance (i.e., harvesting, windstorm/blowdown or wildfire). We cored standing dead trees and logs, when possible, to corroborate death dates associated with past spruce beetle activity (Table 1). At each site, we recorded information on stand structure (e.g., tree size and height, stand characteristics), site characteristics (e.g., elevation, soil characteristics), and disturbance history (e.g., fire history, windstorm/blowdown). Fire-charred trees were sampled opportunistically, when encountered. We also collected bark beetle specimens (Family Scolytidae) from five sites.

Detection of growth releases, mortality dates and stand-level disturbances

Our methods focus on the detection of past spruce beetle activity as inferred from periods of growth releases in the tree-ring record. The method is based upon the assumption that understory spruce will exhibit accelerated growth (a ‘growth release’) when larger diameter, mature trees are attacked and killed by beetles. Our approach likewise assumes that these stand-level growth release events are related to spruce beetle and not other disturbance or climate events. The dominant disturbance agents in spruce forests in south-central Alaska are fire, windthrow and insect outbreaks, although these are not of equal importance on the Alaska Peninsula. In south-central Alaska, fires are typically stand-replacing events with few surviving trees (Rowe and Scotter 1983, Berg and Anderson 2006). Although no long-term paleo fire history data exists for the Alaska Peninsula, the historical record indicates that fires tend to be infrequent and have been a more important disturbance in black spruce (*Picea mariana*) forests than white spruce during the 20th – 21st centuries (National Park Service archives). Windthrow events, which have been documented in Lake Clark NPP as recently as 2007, can cause a similar growth release in understory trees as spruce bark beetle outbreaks. We specifically avoided sites with evidence of stand-level wind damage or selective cutting, and documented evidence of fire (i.e., locations and samples of burned tree poles; evident at only adjacent site near sampling at Telaquana Lake) or other disturbances. Spruce beetle was also evident in the field or had been reported from most of our sampled stands (i.e., Holsten 1993), and no other forest insect is known to preferentially kill mature spruce at a stand-scale (Berg et al. 2006; Holsten et al. 2001).

To verify that the growth release events we observed were not actually climate events (e.g., extreme warming), we ran the same analyses described below on a set of tree cores collected at treeline sites across the Alaska Peninsula (4 chronologies from Lake Clark, Driscoll et al. 2005; 2 chronologies from Katmai, Miller, Berg and Sherriff, unpublished data). These treeline chronologies were developed from cores collected in open spruce stands, without evidence of disturbance, for the purpose of reconstructing local climatic conditions (cf., Driscoll et al. 2005). Trees from open, treeline sites are typically used to construct climate chronologies because they should not show accelerated growth releases when an adjacent tree is lost from the canopy (e.g., due to insect attack or other disturbance). Thus, these treeline chronologies were not expected to show the same release dates as our sites, unless our sites showed releases that represented similar patterns of extreme low-frequency (decadal to multi-decadal) climate variability.

Tree cores were mounted and sanded, and tree-ring widths were counted under a stereomicroscope and measured to 0.01 mm using a combination of standard manual dendrochronological procedures (Stokes and Smiley 1968, Fritts 1976, Cook et al. 1990) and digital dendrochronological procedures using a scanner and the WinDendro software system

(Regent Instruments, Inc.). Each ring-width series (tree core) from each site was visually cross-dated and run through COFECHA (Holmes et al. 1986), which detects measurement and cross-dating errors by computing correlation coefficients between overlapping segments from each individual series. Independent chronologies from neighboring sample sites and published tree-ring chronologies (Driscoll et al. 2005) within the study area were used for cross-dating cores. If errors in cross-dating could not be resolved, the core was excluded from further analysis.

We used the cross-dated chronologies from each site to detect past growth releases using the JOLTS program (R.L. Holmes, University of Arizona, unpublished software), following procedures used by Berg et al. (2006). JOLTS detects growth releases for individual trees by comparing a ratio of the mean growth-ring width for a window of years prior to and following each tree ring, excluding a selected number of the first and last years of each series. For each tree, we excluded the first and last 10 years, and we used a 10-year window and a ratio of ≥ 2.0 to detect growth release years associated with spruce beetle outbreaks (Berg et al. 2006). The detection of individual release years was similar using both 5-year and 10-year windows (Sherriff, unpublished data), but the 10-year window is more conservative and should capture the most severe stand-thinning events, presumably associated with higher-intensity spruce beetle outbreaks. For each tree in each stand (site), the first year of each 10-year period of $2.0\times$ growth was identified as the release event year. We excluded the years within 10 years of a release event year to ensure that release dates were truly independent.

Following the identification of individual growth release years, we calculated the probability of observing a release event in each stand using the binomial statistical model (Ross 1988; Berg et al. 2006) for years that exceeded the $2.0\times$ growth threshold (described above). We first estimated the overall probability of a release by calculating the ratio of the total number of releases in all trees to the total number of available tree years. Secondly, for each year we calculated the number of trees with a release and the number of “recorder” trees in the stand available for release. We use the term “recorder” to indicate the number of trees available to record release events during each year, based on the exclusion of years mentioned above. We then used the binomial model to compare observed release events to expected release events for each year in each stand (cf. Berg et al. 2006). Significant stand-level release years were identified when $> 5\%$ of the recorder trees (and > 3 trees) recorded a growth release in an individual year (using a minimum of 20 recorder trees for identifying significant releases).

Detection of spruce beetle outbreaks

At a stand-scale, we examined the effects of spruce beetle outbreaks by: (1) identifying significantly higher than expected growth release years (representing stand-thinning events) documented by the bimodal model (stand-level release years); (2) examining the percentage of trees with growth releases during individual years and by decade beyond background levels (i.e., decades that include high percentages of trees releasing and significant release years); (3) producing a site-level tree-ring growth chronology to visually examine major stand-level release events; and (4) corroborating the timing of tree death dates with stand-level release years and other evidence of spruce beetle activity (i.e., blue stain and beetle galleries on outer wood). Each site-level chronology was developed from all cross-dated series, in which each series was standardized by dividing individual ring widths by the mean series ring width (Veblen et al. 1991, Eisenhart and Veblen 2000).

Extending the applications of bivariate event analysis (BEA; K1D software; D. Gavin, *unpublished software*), we evaluated both stand-scale effects and regional-scale synchrony of spruce beetle outbreaks. BEA is a temporal modification of spatial point pattern analysis (Ripley's K function; Ripley 1977, Diggle 2003) for one-dimensional time series data and has been previously used to evaluate synchrony among fire events in sedimentary records (Gavin et al. 2006), temporal lags between drought-tree mortality events (Bigler et al. 2007) and fire-climate events (Schoennagel et al. 2007). At a stand-scale, we used BEA to examine temporal synchrony of the initiation of beetle-caused tree death dates and significant growth releases attributed to outbreaks at individual sites (i.e., timing of growth releases following death dates). We limited our analysis to tree death dates with evidence of beetle activity (i.e., blue stain) that occurred within a 10-year period prior to significant growth release years. Next, we used BEA to compare chronologies among sites to examine regional synchrony of spruce beetle outbreaks throughout the Alaska Peninsula. In this case, we used BEA to examine temporal synchrony in the initiation year of significant growth release periods across the 15 sites. The K function was transformed to the L function, $L_{AB}(t)$, where values > 0 suggest synchrony and values < 0 suggest asynchrony in outbreak events within a window of t years. The L function was calculated for 1000 Monte Carlo simulations that determined the 95% confidence intervals for $L_{AB}(t)$.

We also assessed the severity of past beetle outbreak events, using observations of recent growth releases in live trees from three sites (Pedro Bay, Pile Bay and Polly Creek) that survived high-severity ($> 70\%$ mortality of mature trees) beetle outbreaks since the 1990s. Release events affecting $\geq 30\%$ of the live trees within a single decade or a sustained release period across multiple decades were likely moderate- to high-severity disturbances. Release events affecting $< 30\%$ of the live trees during a single decade were likely low-severity disturbances (i.e., small patches of mortality from spruce beetle activity or other disturbance). Our severity categories should be interpreted cautiously because of the dynamic nature of tree-ring records (i.e., removal of recorder trees by subsequent disturbances) and stand structure characteristics over time.

Spruce beetle outbreaks and climate variability

Climate data sets

As an initial examination of the long-term relationship between beetle activity and climate variability, we compared our regional dataset of insect outbreaks across the Alaska Peninsula with three climate reconstruction records: (1) a tree-ring index from the northern Alaska Peninsula of temperature and precipitation correlated with the King Salmon instrumental record from 1947-2000 (Portage_neg index; Driscoll et al. 2005); (2) an El Niño-Southern Oscillation (ENSO) index (NINO3 region; D'Arrigo et al. 2005); and (3) a Pacific Decadal Oscillation (PDO) index (PDO; D'Arrigo et al. 2001). Both ENSO and PDO are characterized by oscillations of warm (positive) and cool (negative) phases of sea surface temperatures, at periodicities of 2 to 6 years and 20 to 30 years, respectively (Diaz and Markgraf 2000; Mantua et al. 1997). We extended the NINO3 and PDO reconstructions through 2005 using methods described in Schoennagel et al. (2007). The procedure involved adjusting the standard deviation and mean of the reconstruction over the period of overlap between the two time series to reflect the detrended instrumental record (detrended values are the residuals from linear regression).

The reconstructed time series was replaced by the instrumental record from 1950 – 2005 when the correlation between the two records was relatively high.

Beetle-climate analysis

For the period spanning 1800-2003, we selected initiation dates of significant stand-level release periods to evaluate with the climate indices. Widespread release years were defined as initiation dates for stand-level releases that occurred at two or more sites. These years were consistent across various window lengths (i.e., 5- and 10-year release periods) and growth thresholds (i.e., 1.75-2.0 growth release). By using the initiation year of growth releases that occurred at multiple sites, we were able to evaluate climate conditions in the years during and prior to widespread beetle outbreaks across a variety of temporal scales. To evaluate the influence of climate variability on insect outbreaks, we used Superposed Epoch Analysis (SEA; Baisan and Swetnam 1990; Grissino-Mayer 1995) to evaluate inter-annual scale relationships, and BEA to evaluate multi-decadal to centennial scale relationships.

At an inter-annual scale, SEA was used to compare climate conditions during release and non-release years based on the climate proxies. Mean values of climate conditions were calculated for each year in a window of 10 years preceding and during widespread release years. To compare average climate conditions with conditions surrounding release event years, 1000 Monte Carlo simulations were conducted in which random years were selected and the expected mean values of climate conditions were calculated over the entire record. Statistical significance was evaluated by a bootstrap method that determined the 95% confidence intervals of the expected mean value of the climate parameter (Mooney and Duval 1993; Grissino-Mayer 1995).

At inter-annual to centennial scales, we used BEA to examine the temporal synchrony between extreme climate events and outbreak events, assuming a one-directional relationship in which outbreaks respond to past and current climate events, but not future climate events. BEA has the ability to test low-frequency temporal relationships and avoids problems with serial autocorrelation by selecting a subset of climatic events rather than using a continuous climate series (e.g., Schoennagel et al. 2007). We compared widespread release years with each climate record using a range of thresholds to define extreme climatic events (i.e., highest and lowest 25%, 15% and 10% of annual values from 1800-2003). We present only the significant results for the highest or lowest 10% ($n = 20$) climate events, although results across thresholds defining climate events were similar.

Results

Spruce beetle outbreaks and climate variability

Evidence for past spruce beetle outbreaks comes from 1299 cross-dated tree cores (91% of the collected tree cores) collected across 15 sites (Table 1). All stands showed at least one significant stand-level growth release over the approximately 200-240 year record (Fig. 2). Across all sites, intervals between significant release periods attributed to bark beetle disturbance ranged from 19 to 127 years, with a mean of 55 years (median of 59 years). Across 6 sites with clear evidence that tree death dates (1910 to 2003) were related to spruce beetle activity (i.e., blue stain, galleries), BEA indicated that significant stand-level growth releases tended to initiate within two years following the tree death dates (Fig. 3; five release events, 17 death dates). The synchrony in death dates and release events support our interpretation that the growth releases are related to spruce beetle damage rather than other types of disturbances (e.g., wind, fire or other). We found no evidence of fire or other disturbances that coincided with the significant growth releases.

Table 1. Study sites on the Alaska Peninsula.

| Site | Dominant Species | No. Trees Sampled (Crossdated Cores) | No. Dead Tree Cores ¹ | Chronology Length ² | Stand Condition of <i>Dendroctonus</i> infestation ³ |
|------------------------------------|------------------------------|---------------------------------------|----------------------------------|--------------------------------|---|
| Two Lakes (TW) | <i>Picea glauca</i> | 88 (86) | 7 | 1635 - 2005 | Light infestation |
| Telaquana Lake – Straty Cabin (ST) | <i>Picea glauca</i> | 121 (96) | 1 | 1797 - 2005 | No evident infestation |
| Telaquana Lake – Braden Cabin (BR) | <i>Picea glauca</i> | 65 (55) | 1 | 1723 - 2005 | No evident infestation |
| Lachbuna Lake (LA) | <i>Picea glauca</i> | 65 (54) | 14 | 1748 - 2005 | Light infestation |
| Tlikakila River (TL) | <i>Picea glauca</i> | 85 (72) | 8 | 1738 - 2005 | Light infestation |
| Currant Creek (CU) | <i>Picea glauca</i> | 80 (75) | 12 | 1744 - 2005 | Light-moderate infestation |
| Pedro Bay (PE) | <i>Picea glauca</i> | 95 (80) | 78 | 1770 - 2005 | High infestation |
| Polly Creek (PO) | <i>Picea glauca x lutzii</i> | 120 (120) | > 100 | 1698 - 2000 | High infestation |
| Pile Bay (PI) | <i>Picea glauca</i> | 94 (66) | 70 | 1709 - 2005 | High infestation |
| Chinitna Bay (CH) | <i>Picea glauca x lutzii</i> | 121 (115) | 13 | 1638 - 2005 | Light infestation |
| Coville Lake East (CO) | <i>Picea glauca</i> | 91 (85) | 65 | 1794 - 2006 | High infestation |
| Bay of Isles 1 (BI1) | <i>Picea glauca</i> | 89 (88) | 79 | 1821 - 2006 | High infestation |
| Bay of Isles 2 (BI2) | <i>Picea glauca</i> | 88 (86) | 81 | 1833 - 2006 | High infestation |
| Lake Brooks (LB) | <i>Picea glauca</i> | 95 (91) | 7 | 1828 - 2007 | Moderate infestation |
| Valley 10,000 Smokes (VS) | <i>Picea glauca</i> | 127 (127) | 14 | 1696 - 2007 | Light infestation |

¹ These are included in No. Trees Sampled.

² minimum 1 tree in chronology

³ Beetle severity level - low < 30% tree mortality; moderate 30-70% tree mortality; high > 70% tree mortality

However, the eruption of Novarupta in 1912 caused significant short peaks in growth (generally < 10-year periods) that initiated between 1913-1915 at all five sites in Katmai (Colville East, Bay Isles 1 – 2, Lake Brooks, and Valley 10K Smokes; Fig. 4). These growth responses following the 1912 eruption are ecologically significant, but were excluded from the current analysis.

Across the 15 sites on the Alaska Peninsula, the initiation of growth-release events attributed to beetle outbreaks were synchronized at 0-15, 20, 23-27, 73-76, and 108-133 years (Fig. 5).

Within these synchronized outbreak periods, the initiation of growth releases tended to occur within a few years of one another across stands (up to 300 km north-south between sites), and

many sites initiated growth release periods during the same year (Fig. 2). At multi-decadal scales, four or more sites initiated significant growth release periods in the 1810s, 1830s, 1870s, 1900-1910s, and late 1970s-early 1980s (Figs. 2 and 4). Recent activity at various infestation levels since the late 1990s and early 2000s was evident at 13 of 15 sites (Table 1).

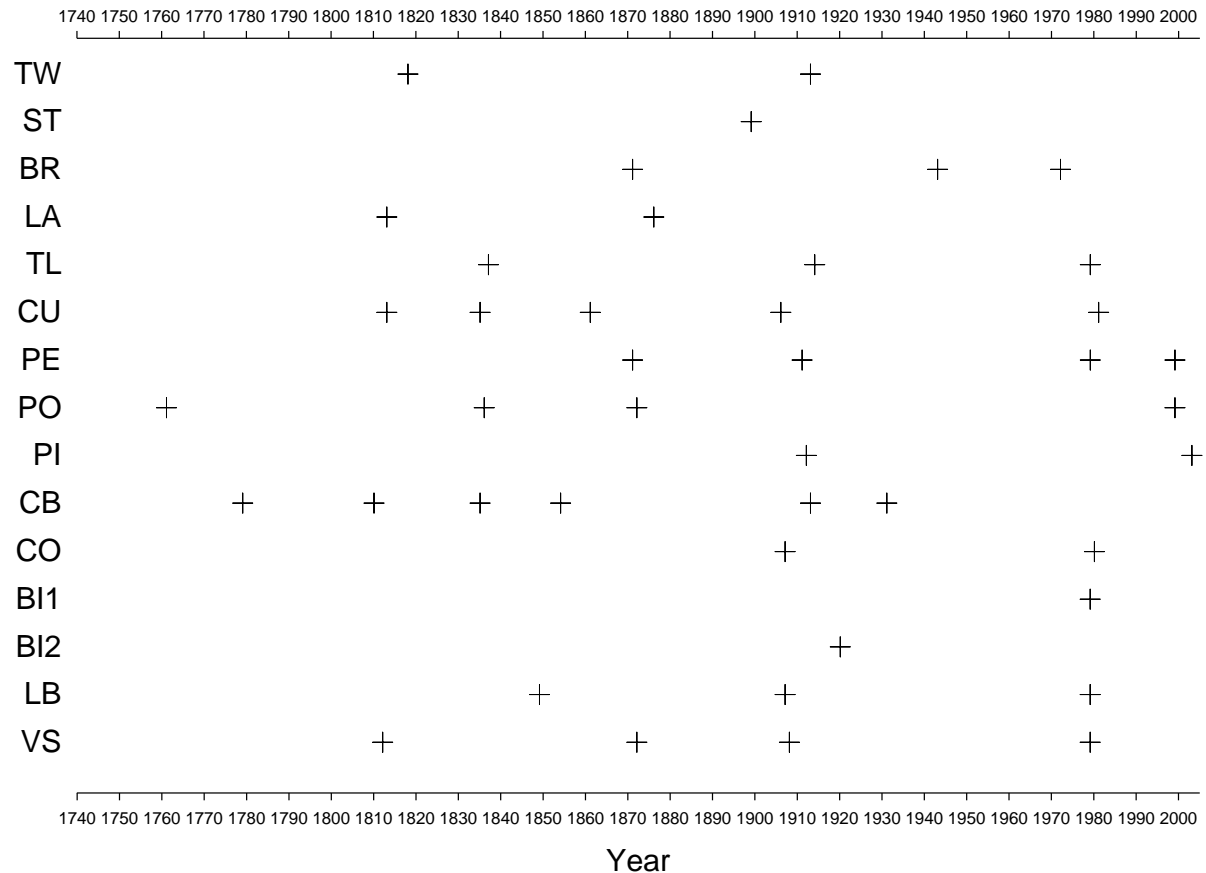


Figure 2. Initiation years of significant (> 2.0) growth release periods attributed to spruce beetle activity at individual stands (+) shown on the y-axis from north to south on the Alaska Peninsula. Initiation years in 1999 – 2002 are (> 2.0x) growth releases at the stand-scale following recent spruce beetle activity for at least 3 years but less than 10 years from sampling (Sites: PE, PO, PI). Peaks in growth related to the 1912 Katmai eruption at sites in Katmai NPP (CO, BI 1-2, LB, VS) were excluded (see the Results section and Figure 4: k – o).

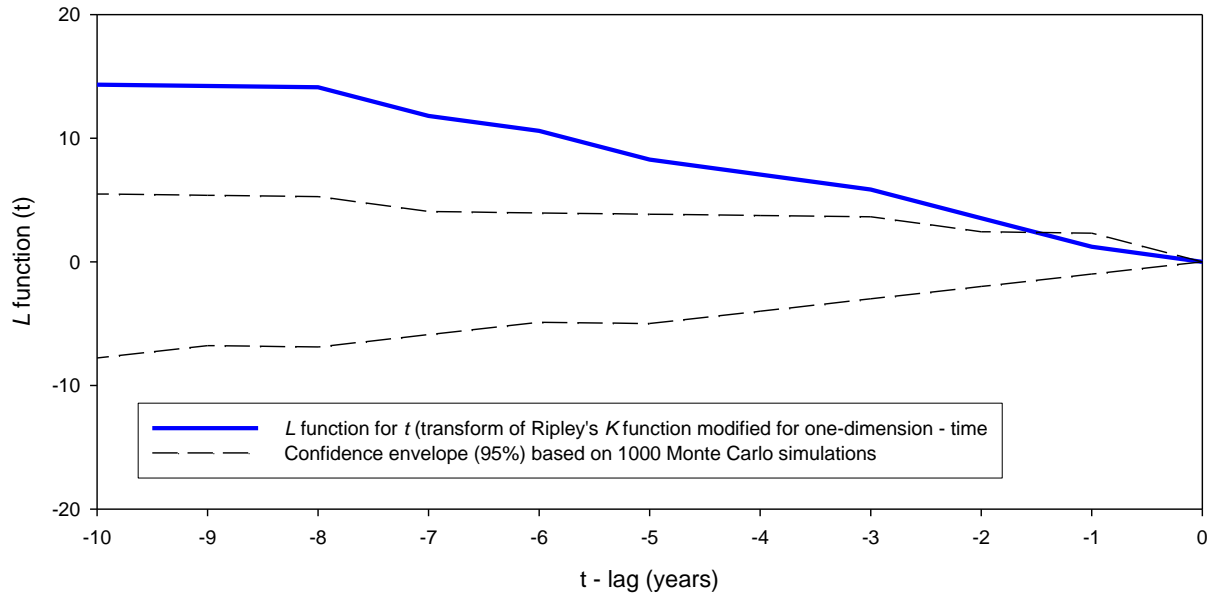
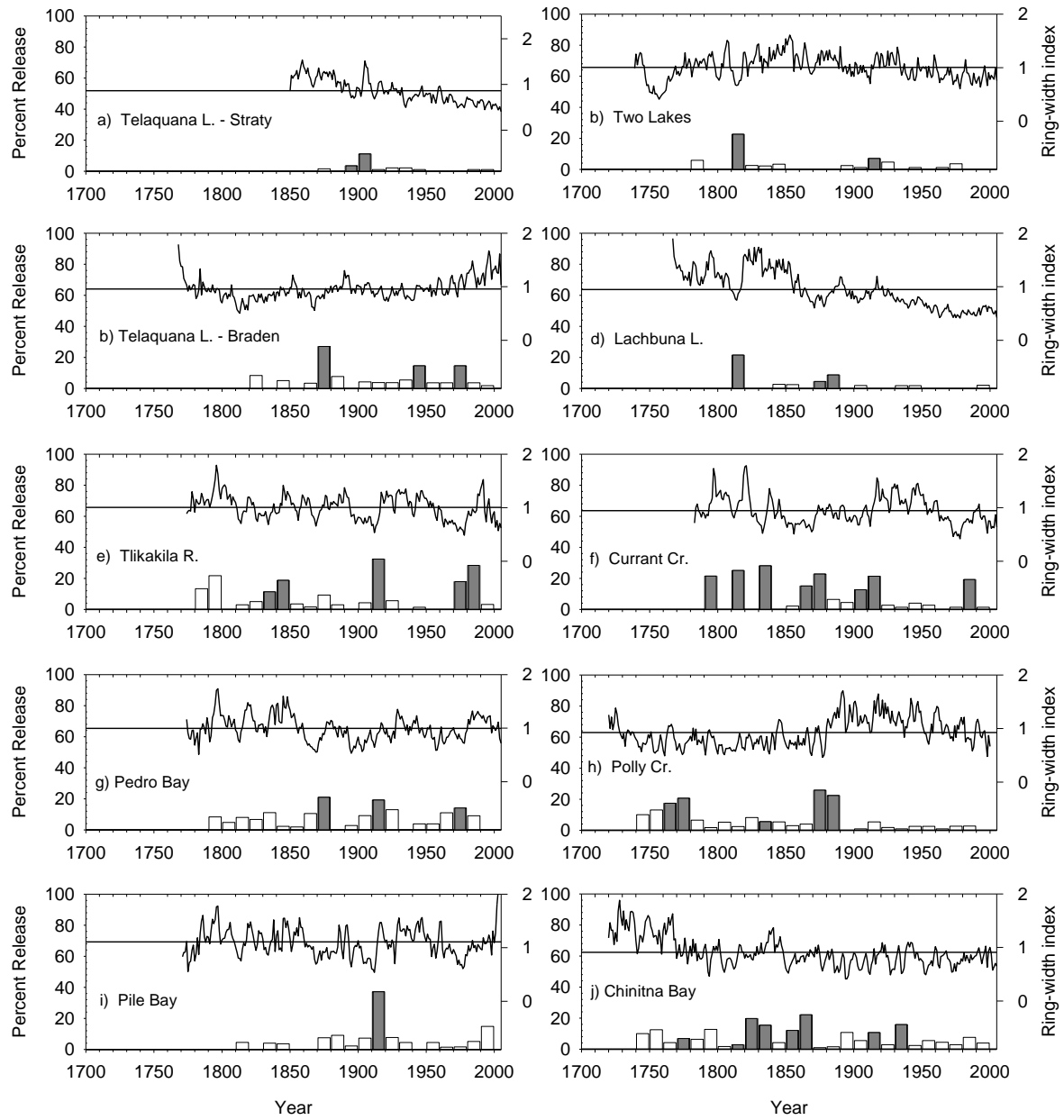


Figure 3. Bivariate Event Analysis (BEA) results of synchrony in beetle-caused death dates and significant growth releases at six sites with evidence of beetle damage (5 release dates and 17 death dates between 1910-2003). The solid blue line is the K-function transformed to the L-function, $L_{AB}(t)$, where values >0 indicate synchrony and <0 , asynchrony, in death dates and growth releases. The dashed lines represent the 95% confidence envelope.

Past stand-thinning events attributed to spruce beetle activity varied greatly in severity across sites and at different time periods. All stands showed periodic, low-severity disturbances in which less than 30% of the live trees recorded growth releases (Fig. 4). These low-severity disturbances are interpreted as low levels of spruce beetle activity when our methodological criteria are met (i.e., significant percentage and sustained growth releases on live trees). For example, low to moderate severity outbreaks in the 1810s and 1970s-1980s were recorded across 5 or more dispersed sites, respectively (Figs. 2 and 5). During other time periods (i.e., 1870s and 1900-1910s), growth release evidence suggests the effects of spruce beetle outbreaks were of moderate to high severity ($> 30\%$ of the trees with sustained growth releases) across many sites on the Alaska Peninsula (Fig. 4).

Corroborating evidence that significant growth releases are associated with spruce beetle outbreaks is the comparison of growth release events within our 15 closed-canopy stands and six nearby treeline sites (Driscoll et al. 2005; R. Sherriff, unpublished chronologies). Across the Alaska Peninsula, at least two of the six treeline sites record significant releases in the 1930s (2 sites), 1940s (2 sites) and 1990s (3 sites; figure not shown); none of which are widespread release periods in our closed-canopy stands (Figs. 2 and 4).



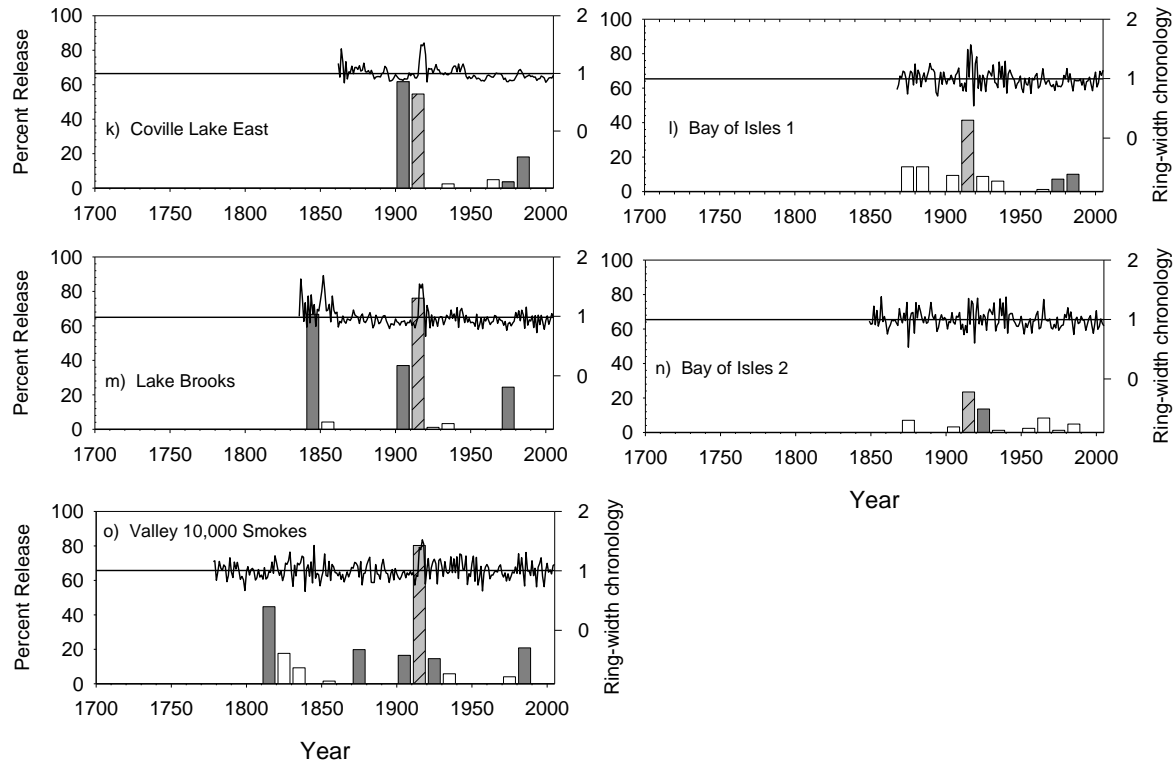


Figure 4. The percentage of trees by decade with years that exceed the 2.0x growth threshold for a minimum of 10 years compared to the previous 10 years (histogram; left axis). Dark grey bars indicate decades with years of significantly more release events ($> 5\%$ recorder trees and a minimum of 3 trees) than expected attributed to spruce beetle outbreaks or other potential stand-level disturbance events (white bars illustrate the percentage of trees with non-significant growth releases by decade). Hatched light grey bars represent the percentage of trees in the 1910s showing significant growth release years following the 1912 Katmai eruption at sites in Katmai NPP (k – o). Ring-width chronologies (line graph; right axis), which illustrate growth trends are shown only for the period with a minimum of 10 trees.

The lack of synchrony between our chronologies (Fig. 4) and the treeline chronologies indicates that the release periods identified in our closed-canopy stands are not solely a response to low-frequency climate variability, but a response to stand-thinning events attributed to spruce beetle outbreaks. The lack of direct influence of climate on significant growth trends does not, however, exclude climate as a driver of insect outbreaks.

Spruce beetle outbreaks and climate variability

Detectable relationships between climate variability and the initiation of growth releases responding to spruce beetle outbreaks were primarily evident at an inter-annual scale. Across the 15 sites on the Alaska Peninsula, warm winter-spring and dry late summer conditions, as inferred from the Driscoll et al. (2005) chronologies, occurred more often than expected 1 year prior to the initiation of local (1 site; $n = 31$ years; not shown) and widespread (≥ 2 sites; $n = 7$ years) release years from 1800-2003 (Fig. 6a). The warm-phases of ENSO (El Niño) and PDO occurred 1 and 2 years, respectively, prior to the initiation of widespread release years (Fig. 6b-

c), but no significant relationships were detected for local (1 site) release years (*data not shown*). BEA results suggest that the initiation of widespread beetle-caused release events tend to occur following a 10-12 year period of the highest 10% values of warm-phase ENSO and warm-phase PDO indices (highest growth years of either indices; $n = 34$ years), although only years 2-3 were significantly associated with the warm phases of ENSO or PDO. No detectable synchrony of beetle outbreaks and combined phases of ENSO and PDO were identified, which may, in part, be due to the limited number of widespread outbreak years ($n = 7$) in which to examine combined phases of ENSO and PDO conditions.

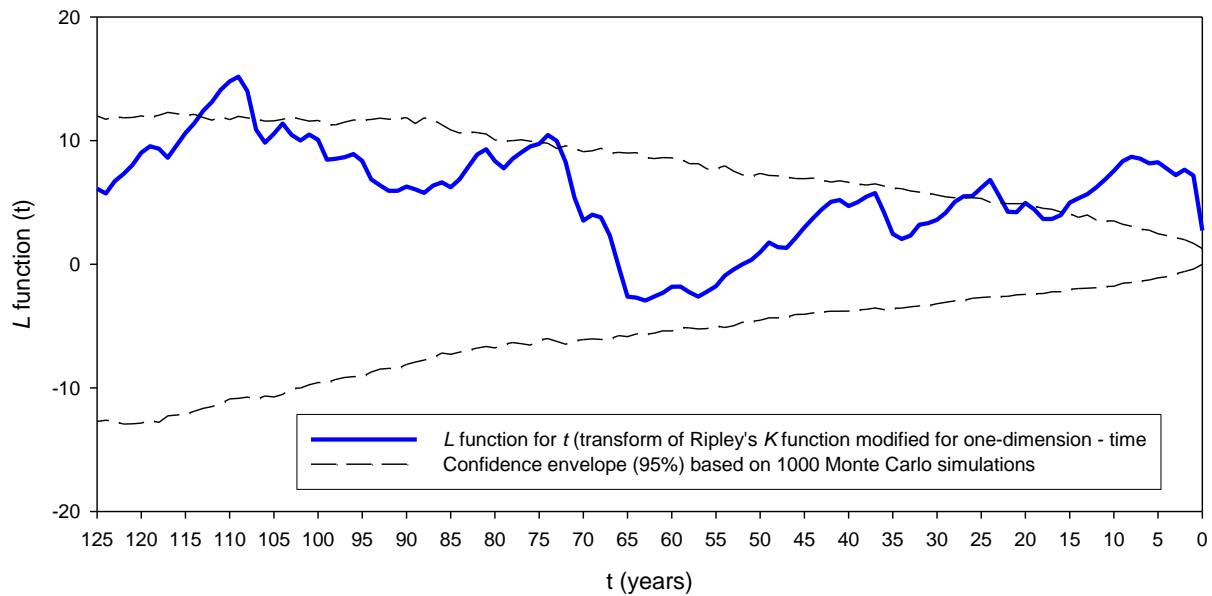


Figure 5. BEA results of synchrony in the initiation of growth release events attributed to spruce beetle outbreaks across 15 sites on the Alaska Peninsula. The solid blue line is the K function transformed to the L function, $L_{AB}(t)$, where values >0 indicate synchrony, and <0 , asynchrony, in outbreak events. The dashed lines represent the 95% confidence envelope.

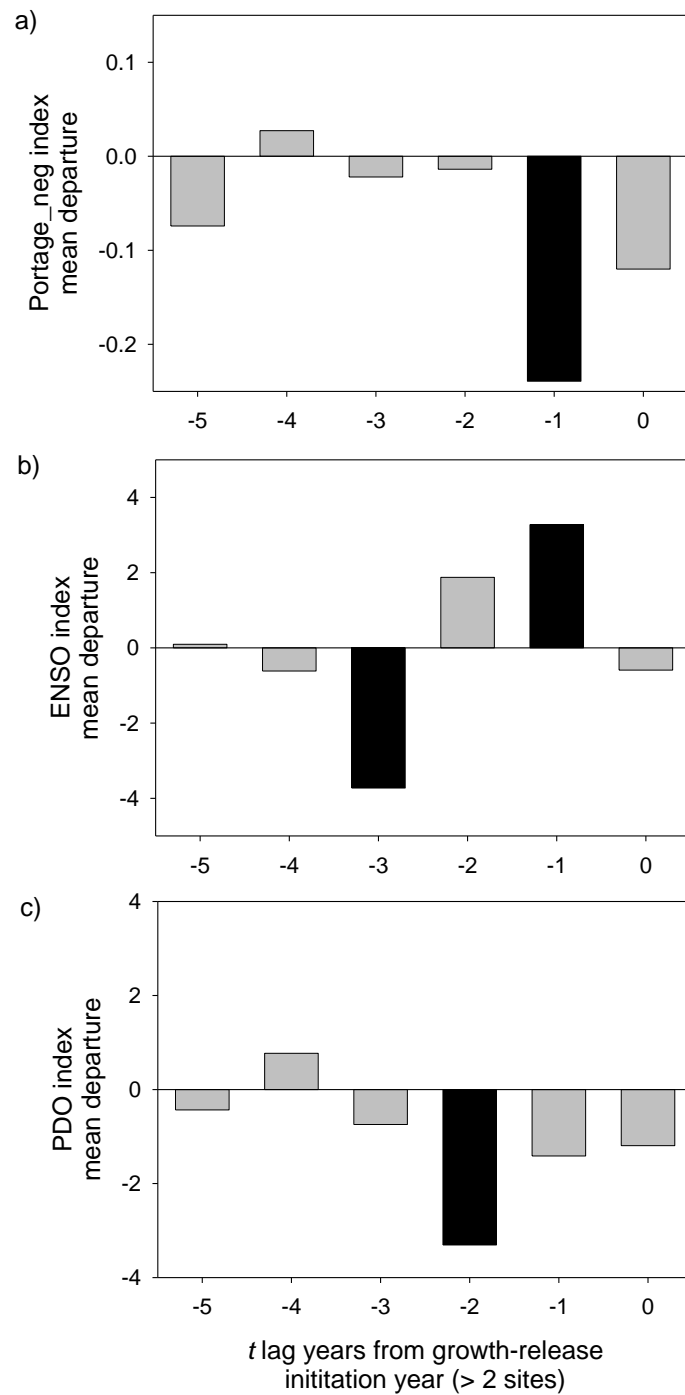


Figure 6. Mean departures of the climate indices from 1800-2003 of a) temperature and moisture (Portage – neg.; Driscoll et al. 2005); b) El Nino-Southern Oscillation (ENSO; D’Arrigo et al. 2005); and c) Pacific Decadal Oscillation (PDO; D’Arrigo et al. 2001). Black bars indicate significant departures from the mean (95% CI).

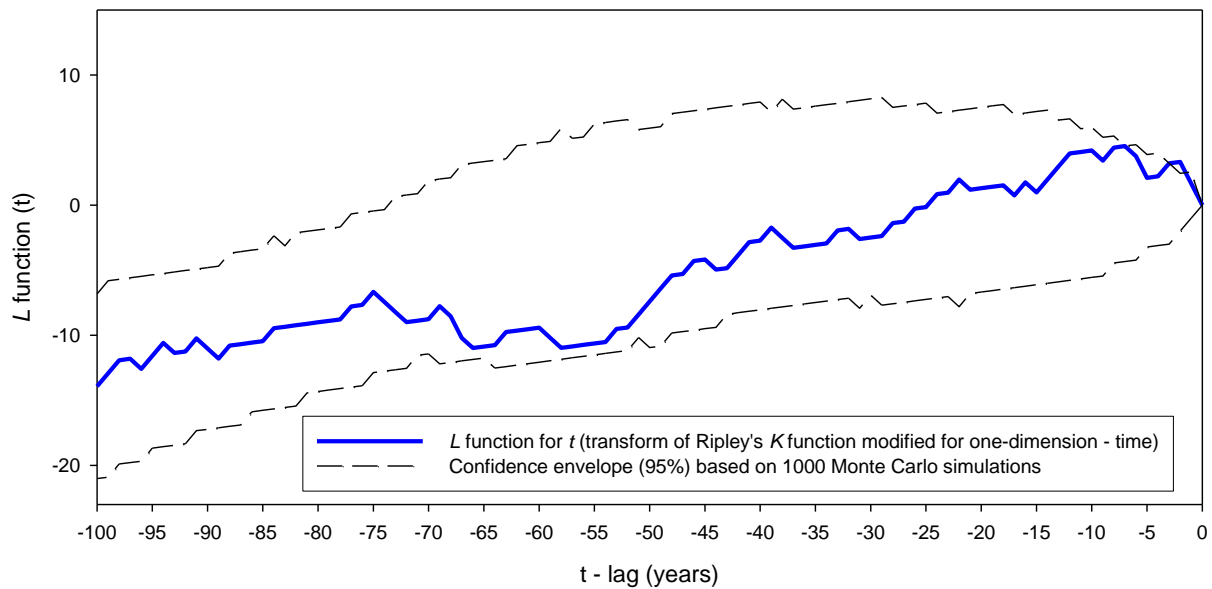


Figure 7. BEA results of synchrony in the initiation of widespread growth-release events attributed to spruce beetle outbreaks (> 2 sites; $n = 7$ years) and the highest 10% values of warm-phase ENSO and warm-phase PDO indices ($n = 34$ years). The solid blue line is the K function transformed to the L function, $L_{AB}(t)$, where values > 0 indicate synchrony and < 0 asynchrony in outbreak events. The dashed lines represent the 95% confidence envelope.

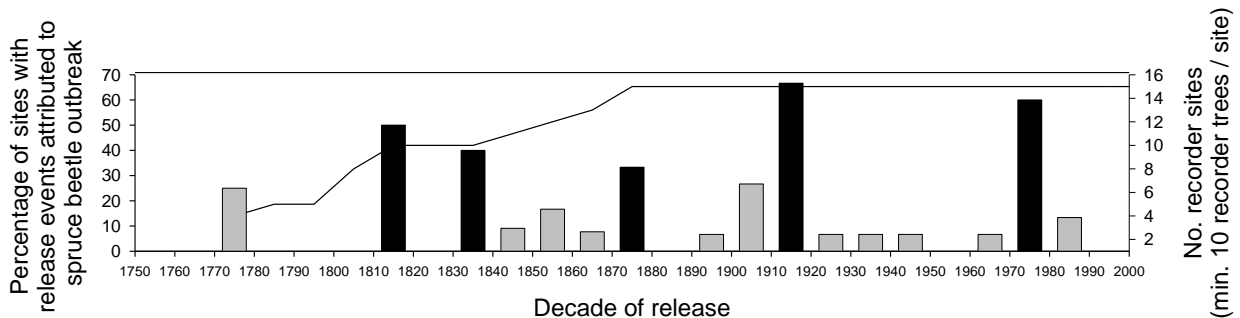


Figure 8. The percentage of sites on the Alaska Peninsula with significant release events, by decade (histogram bars; left y-axis). Black bars indicate decades in which ≥ 3 or more sites recorded a growth release. The solid horizontal line represents the number of sites recording insect outbreaks through time (right y-axis).

Discussion

Current stand-level conditions and insect activity on the Alaska Peninsula

Drivers of the recent spruce beetle outbreak in south-central Alaska are thought to include warmer than average summer temperatures, drought, and host stand susceptibility (Berg et al. 2006). South-central and southwest Alaska have been affected by epidemic levels of the spruce bark beetle since the 1990s, although a large portion of the northern interior of the Alaska Peninsula has shown only moderate to background levels of spruce beetle damage. At several interior sites in Lake Clark (Two Lakes, Telaquana, Lachbuna), we found dead and damaged trees heavily infested by an unidentified species of engraver beetle (*Ips* sp.), whereas spruce bark beetle (*Dendroctonus rufipennis*) levels were low to undetectable. Previous spruce beetle activity along the Tlikakila River was also documented in the 1950s and 1980s (Holsten 1993), but the mouth of the Tlikakila, where it enters Lake Clark, showed only light infestation when we sampled in 2005. Spruce beetle activity in Katmai has accelerated more recently (2006-2007) and has centered on the mature stands surrounding Lake Brooks, Colville, and Naknek (Lundquist 2007). Many mature forested areas in interior areas of Katmai (Coville, Bay of Isles), Lake Iliamna (Pedro Bay, Pile Bay), and coastal Lake Clark (Polly Creek) have been heavily impacted (> 75% mortality), whereas other sites have shown only moderate damage (< 50%) or background (< 20%) levels of beetle infestation. Coastal and near-coastal areas of the northern Peninsula have also experienced extensive mortality. Southern (Pedro Bay, Pile Bay) and eastern (Polly Creek) sites in and near Lake Clark were heavily impacted (> 70% mortality), but beetle activity in 300-400 year old trees at Chinitna Bay has remained light into 2008, in spite of recent (2006) beetle-kill approximately 15 km to the east.

Spruce beetle outbreaks in south-central Alaska

Previous research on the Kenai Peninsula has shown that over the last 250 years, stand-thinning events attributed to spruce beetle outbreaks occurred commonly among spruce forests at a mean return interval of 52 years (Berg et al. 2006). Tree-ring studies from the Kenai Peninsula indicate that regional episodes of beetle-caused thinning occurred several times during the 1800s and 1900s (Berg et al. 2006). All stands on the Kenai show evidence of spruce beetle outbreaks, and several stands show evidence of regional outbreaks during the 1810s, 1850s, 1870s-1880s, 1910s, and 1970s-1980s. However, these previous outbreaks are not believed to have been as severe as the 1990s outbreak that killed most of the mature white and Lutz spruce in the region (Berg et al. 2006). The Kenai Peninsula has also seen an increase in spruce beetle activity in recent years, with a doubling of beetle-impacted area (current beetle activity) between 2005-2006. The present study expands the current knowledge on the history of spruce beetle activity to the Alaska Peninsula and provides a broader regional context of disturbance throughout south-central and southwest Alaska.

Tree-ring evidence indicates that stand conditions (i.e., optimal host trees) and connectivity (i.e., adjacency of homogeneous stands) on the Alaska Peninsula were historically sufficient to support regional-scale coalescence and spread of epidemic levels of spruce bark beetles when climate conditions were conducive. Initiation dates of spruce beetle outbreaks were synchronized at inter-annual to centennial scales, and often occurred within 0 to 2 years of each other. Our results, in combination with evidence from the Kenai Peninsula (Berg et al. 2006),

indicate that extensive spruce beetle outbreaks have occurred in synchrony since at least the early 1800s across south-central and southwest Alaska.

Across all stands in our study, growth-release events attributed to spruce beetle activity occurred at a mean return interval of 55 years over the last 200-240 years, nearly identical to the average return interval for the Kenai Peninsula (52 years). Likewise, regional events (≥ 3 sites) on the Alaska Peninsula in the 1810s, 1830s, 1870s, 1900-1910s, and 1970s attributed to spruce beetle activity match regional outbreak dates on the Kenai Peninsula (see Fig. 8 and Berg et al. 2006). For example, 17 of 23 sites on the Kenai Peninsula and 6 of 15 sites on the Alaska Peninsula showed significant release periods during the 1870s-1880s. Many other sites also recorded growth releases during this period, but did not meet our significance criteria, perhaps due to light infestations or young stand ages (i.e., lack of suitable stand structural conditions at individual sites; Berg et al. 2006 and unpublished data). The extensive synchrony of beetle activity and high levels of mortality observed during the recent outbreak (late 1970s-present) appear to be unprecedented when compared with our reconstructions of historic (pre-1970s) spruce beetle outbreaks.

The spruce forests on the Alaska Peninsula show that past stand-thinning events attributed to spruce beetle activity varied greatly in severity across sites and at different time periods. In our study, all stands showed periodic, low-severity disturbances in which less than 30% of the live trees recorded growth releases (Fig. 4). Synchrony in higher-severity outbreaks is also evident in the past. The effects of spruce beetle outbreaks in the 1870s and 1910s were of moderate to high severity ($> 30\%$ of the trees with sustained growth releases) across many sites (see Fig. 4 and Berg et al. 2006). At most sites on the Kenai Peninsula, more than 50% of the trees showed a release during these two time periods (Berg et al. 2006). However, Berg et al. (2006) conclude that forest mortality associated with the 1870s-1880s outbreak was not as extensive as that in the 1990s, based on an expected relationship between mortality and growth releases.

A couple of issues constrain our ability to evaluate the severity of previous outbreaks. First, extensive mortality since the 1970s and 1990s may limit our ability to accurately identify the severity of previous disturbances due to the rapid decay of “recorder” trees. Secondly, a growth release in the tree-ring record may lag a beetle outbreak by one to many years because of variation in tree density, stand age, and number of subcanopy trees, among other factors. Thus, the use of growth releases for assessing the severity of spruce beetle activity may result in an underestimate of mortality.

Our interpretations of disturbance severity are based on comparisons between death dates in beetle-killed trees and the timing of growth releases observed in surviving trees, as measured at three sites that showed $>70\%$ mortality. Although results from this study and Berg et al. (2006) suggest that moderate or higher severity spruce beetle outbreaks were common in the past, they also indicate that the recent outbreak may be of unprecedented severity (i.e., higher tree mortality). Further research is necessary to fully characterize the effects of the current beetle outbreak (i.e., extent, severity, and effects on regeneration).

Spruce beetle outbreaks and climate variability

Across south-central Alaska, a significant association between warmer temperatures and the eruption of epidemic beetle outbreaks is evident. On the Kenai Peninsula, spruce beetle outbreaks since 1971 have been correlated with short-term (5-6 yr) periods of unusually warm summer temperatures in the instrument record (Berg et al. 2006). Consecutive summers of above-average temperatures are believed to increase the rate of spruce beetle reproduction and at the same time increase drought stress on host trees (Juday et al. 2005; Berg et al. 2006). However, instrumental records rarely exist before the mid-20th century, making it difficult to examine potential temperature-beetle interactions in the past. As a result, our understanding of the long-term relationship between climate variability and beetle activity across temporal scales has been limited.

Our results suggest a pattern of high-frequency climate conditions (multi-year warm and dry periods) preceding epidemic levels of regional spruce beetle activity on the Alaska Peninsula since the 1800s. Decades of regional spruce beetle outbreaks (1810s, 1830s, 1870s, 1900-1910s and 1970s, 2000s) initiated during and following years with above-average December-March temperatures and below-average August precipitation (Fig. 6). The combined effects of temperature and precipitation can have an important indirect effect of moisture stress, reducing the ability of host trees to resist beetle attacks (Berg et al. 2006, Raffa et al. 2008). Additionally, warmer winter-spring temperatures support higher beetle population survival, and may also allow the beetles to complete their life cycle within one year rather than the normal two-year period, although accelerated development is most often linked to unusually warm summer temperatures (Werner and Holsten 1985; Juday et al. 2005; Berg et al. 2006). Summer temperatures may also be an important driving factor for beetle outbreaks on the Alaska Peninsula, but are not evident from the reconstructed climate indices.

Over the past 200 years, warm conditions that have preceded widespread spruce beetle outbreaks have been strongly associated with the warm-phases of ENSO (El Niño) and PDO. Our findings illustrate the importance of high-frequency (inter-annual) warming associated with El Niño events on insect outbreaks during the dominant cool-phase (and cooler) conditions of PDO (i.e., 63% of years from 1800-2003; D'Arrigo et al. 2001). A lag of 1 to 3 years following an attack is known to occur before tree death is evident (Juday et al. 2005), which corresponds well with our findings that warm winter-springs and dry late summer conditions associated with warm-phases of ENSO and PDO occurred 1 to 2 years prior to the initiation of beetle-caused growth releases. We hypothesize that there are likely important interactions between ENSO and PDO, and possibly other broad-scale climate mechanisms (e.g., Arctic Oscillation, Atlantic Multidecadal Oscillation), driving warmer temperatures associated with past beetle outbreaks at both inter-annual and multi-decadal scales in south-central Alaska. With increasingly larger datasets and longer records of regional outbreaks throughout south-central Alaska (Alaska Peninsula and Kenai Peninsula) we are beginning to explore these relationships in greater detail.

Given current climate change scenarios, it is possible that areas that have sustained little damage from the bark beetle in the past may be more susceptible to widespread outbreaks today and into the near future, potentially increasing their susceptibility to fire (e.g., Hicke and Jenkins 2008). The degree to which new outbreaks could disrupt ecological processes or vary from past episodes of beetle outbreaks is largely unknown. However, once a beetle outbreak begins, the

climate thresholds supporting the epidemic population explosion may not be as critical, whereas the stand structural characteristics in combination with landscape connectivity are likely the driving limiting factors to sustain an outbreak. A combination of suitable host availability, beetle population dynamics, and weather conditions are necessary drivers for stand- to landscape-scale eruptions of bark beetles to occur (e.g., Raffa et al. 2008). In particular, consecutive years with unusually high temperatures and low moisture conditions are known to promote beetle outbreaks; e.g., drought stress in susceptible tree species greatly increases the probability of infestation (e.g., Werner and Holsten 1985; Juday et al. 2005; Berg et al. 2006). An extended period of unusually warm conditions can also support a shift from a two-year to a one-year life cycle for *Dendroctonus* beetles, allowing for a significant increase in population numbers and spread (Hansen and Bentz 2003, Berg et al. 2006). Thus, multi-year periods of high temperatures and drought conditions, as we have seen in recent years, combined with homogeneous forest structural conditions, often caused by stand-replacing disturbances (i.e., beetle outbreak, fire or wind blowdown), may continue to result in synchronous, spatially disjunct beetle outbreaks that coalesce into regional-scale outbreaks.

Conclusions

In increasingly climatically sensitive ecosystems, such as high latitude boreal forests, it is critical to evaluate if recent warming is contributing to a regime shift in which the frequency, severity, location and extent of insect eruptions exceeds what we can infer from historical outbreak patterns (Logan and Powell 2001; Logan et al. 2003; Hicke et al. 2006; Raffa et al. 2008). An important question to address is whether recent warming has altered the resiliency of forests to beetle attacks (both in terms of outbreak intensity and spread), and limited the forests' ability to retain its historic structural and functional characteristics.

The conclusion from the Alaska Peninsula (this study) and the Kenai Peninsula (Berg et al. 2006) suggests that moderate to high severity spruce beetle outbreaks occurred episodically over the past 250 years across vast areas of south-central Alaska, and were associated with multi-year periods of warm and dry conditions related to El Niño and warm-phase PDO conditions. This indicates that although connectivity of suitable habitat and optimal host trees is important (e.g., Aukema et al. 2006; Raffa et al. 2008), high-frequency (multi-year) climate variability has been the primary driver of widespread, epidemic-proportion outbreaks. The spatial extent of recent eruptions of bark beetle populations appears to be within the historical range of variability in terms of geographic range, but recent outbreaks since the late 20th century show greater synchrony across sites than in the past. Further research is necessary for understanding the spatio-temporal effects of current beetle activity in high latitude forests (i.e., regeneration dynamics and species compositional changes).

This research represents an important beginning to our understanding of the potential divergence between historic and recent epidemic levels of insect outbreaks, as well as the ecological significance of beetle outbreaks in this climatically sensitive ecosystem. The results of this study provide baseline information on current forest structure, and help to define the natural range of variability in insect outbreaks for parks on the Alaska Peninsula.

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The Department of the Interior protects and manages the nation's natural resources and cultural heritage; provides scientific and other information about those resources; and honors its special responsibilities to American Indians, Alaska Natives, and affiliated Island Communities.

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